

PETRORHAGIA (CARYOPHYLLACEAE) OF NORTH AMERICA

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ABSTRACT

As an outgrowth of the discovery of *Petrorhagia prolifera* (L.) P. Ball & Heyw. in Michigan, a review is presented of North American material of *Petrorhagia* (Ser. in DC.) Link, a genus revised by Ball and Heywood (1964). Four species, all introduced from Europe, are ascribed to North America based on field study and an extensive herbarium survey that included European material. The history of introduction (where known), distribution, and current status of each species is presented. Petal vein color is described as an additional character that can be used in distinguishing the three species of the *P. prolifera* complex. A partial synonymy emphasizing names used in major floristic manuals and additional synonyms not listed by Ball and Heywood (1964) is presented to establish a transition to previous treatments.

INTRODUCTION

Introduced plants often receive a very casual treatment in floristic literature, being dismissed by such phrases as "sparingly established in waste places in our range," or "found as a weed here and there in the n. part of our range" (Gleason & Cronquist, 1963). The current distribution of an introduced plant may be quite different than what is recorded in the literature, as shown by Shinnars (1965) in his study of *Holosteum umbellatum* L. Identification of aliens can be problematic since recent introductions may not be represented in regional manuals; see Shinnars (1969), Pringle (1976), and Rabeler (1980) for examples. An evaluation of the documentation, in the literature and in herbarium collections, of the genus *Petrorhagia* (Ser. in DC.) Link in North America shows a similar pattern: frequent misidentifications, species with poorly documented distributions, and a complex nomenclature. The account presented here is aimed at dispelling the confusion surrounding *Petrorhagia* as it exists in North America.

An additional problem encountered in dealing with introduced plants is the ambiguous use of terminology employed to describe their status in a given flora. Robbins (1940) defined two of the most frequently used terms, naturalized and adventive, as follows:

NATURALIZED: "introductions that have been within our borders for a long period, are rather widely distributed, multiply readily, may compete more or less favorably with native species, and behave much as in their own geographical range."

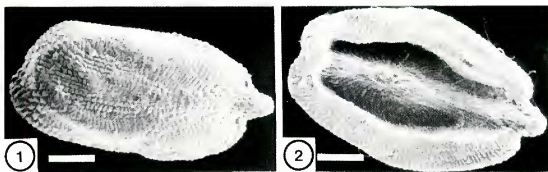
ADVENTIVE: "relatively recent introductions, less widely distributed than naturalized species and not so firmly established."

Depending on the size of the geographic unit considered, both terms could be applied correctly to three of the four species of *Petrorhagia*. For example, *Petrorhagia prolifera* (L.) P. Ball & Heyw. was first collected in North America shortly after 1800 and its current distribution suggests a naturalized species. Yet, collections from Georgia, Tennessee, and Michigan suggest that "adventive" is a better term for these populations. Because the probability of reintroduction from cultivation or other means is relatively high at a given site, a local definition of status of introduction is desirable and will be used whenever possible.

METHODS AND MATERIALS

Many of the data for this study were gathered from herbarium specimens. Five hundred and thirty-one specimens representing North American collections were examined from 82 herbaria (see acknowledgments) [all symbols for herbaria cited follow Holmgren et al. (1981) with the exception of EGV (personal herbarium of Dr. Edward G. Voss)]. Morphological and distributional data presented are based on these specimens. Measurements cited are based on dried materials, using a millimeter rule and an ocular micrometer at 10-30X magnification. For comparative study of *Petrorhagia* from its native environs, 718 Old World specimens from 26 herbaria, including BH, F, MICH, MO, NA, ND, NY, and US were consulted. Field observations and collection of *Petrorhagia* was concentrated in Michigan (1976 - 1982), with brief visits to California (1980), Texas (1980), and Maryland (1981) added for gathering data on *Petrorhagia* species occurring there. Forty-seven voucher specimens documenting this work are deposited at MSC.

The distinctive external morphology of the seeds of these species was examined using two methods. Scanning electron micrographs were taken of the seeds of *Petrorhagia prolifera* (Figs. 1 and 2) and *P. saxifraga* (L.) Link. The seeds were attached to stubs with Tube-Koat adhesive, coated with about 200Å of gold under a vacuum in a sputter coater, and photographed at 30X in an ISI Super Mini SEM. Scanning photomicrographs of the seeds of all four species (Figs. 3-6) were taken at 20X by Darwin Dale using the apparatus described in Dale (1982).



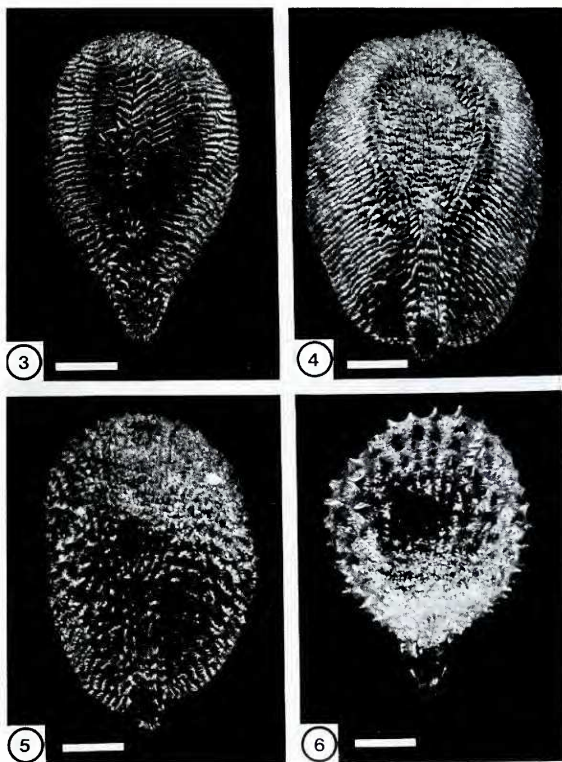
FIGS. 1–2. Scanning electron micrographs of seed surface of *Petrorhagia prolifera*, Michigan, *Rabaler 154* (MSC). Scale = 250 μ m. 1. Dorsal surface. 2. Ventral surface.

HISTORICAL ACCOUNT

The most recent revision of *Petrorhagia* is that of Ball and Heywood (1964), in which 25 species, 4 subspecies, and 4 varieties are recognized. Since the appearance of this work, additional taxa totaling three species¹ (Phitos, 1966; Greuter & Mouterde, 1970; Brullo & Furnari, 1979), two varieties (Damboldt & Phitos, 1972; Huber-Morath, 1977), and one from (Gamisans, 1974) have been recognized. In addition, Greuter and Burdet have published combinations altering the rank of two Ball and Heywood combinations, raising one variety to the species level (in Greuter & Raus, 1982) and one variety to the subspecific level (in Greuter & Raus, 1984). Most *Petrorhagia* species are native to the eastern Mediterranean region, with 16 of the 29 species restricted to local areas of Greece, Crete, and/or Turkey. Only three species, each of which has been introduced in North America, have natural distributions that extend northward into Europe and, thus, out of the Mediterranean climatic regime.²

One problem complicating the status of *Petrorhagia* is the name itself. Most of the species have at some time been placed in the genus *Tunica*. Ludwig published *Tunica* in 1757, but his usage of it as a substitute for *Dianthus* L. (1753) is illegitimate. In American references, authorship of *Tunica* is usually attributed to Scopoli (1772) who also used the name as a substitute for *Dianthus* (Ball & Heywood, 1964). Mertens and Koch (1831) redefined *Tunica*, distinguishing the genus from both *Gypsophila* L. and *Dianthus* on the basis of seed and petal characters. Even in this form, *Tunica* Mertens & Koch remains a later homonym of *Tunica* Ludwig, which is a

¹Two unnecessary combinations have been made: *P. kennedyae* (A. K. Jackson & Turrill) Meikle in 1977 (see Rabaler, 1984) and *P. obcordata* (Margot & Reuter) S. M. Thomas in 1983 (see Rabaler, in press).



FIGS. 3–6. Scanning photomicrographs of dorsal seed surface of *Petrorhagia* spp. Scale = 250 μm . 3. *P. saxifraga*, Michigan, *Rabaler* 262 (MSC). 4. *P. prolifera*, Michigan, *Rabaler* 154 (MSC). 5. *P. nanteuilii*, California, *Bacigalupi, Robbins, & Hoffman* 5676 (JEPS). 6. *P. velutina*, California, *Serpa s.n.* (MSC).

synonym of *Dianthus* (Ball & Heywood, 1964). Therefore, *Tunica* must be rejected as illegitimate under Article 64 of the International Code (Voss et al., 1983). Maire (1963) used *Tunica* and cited "*Tunica* Boehm. in Ludw. (1760), *nom. abort.*, *emend.* Mert. et Koch (1831); *nom. conserv.*" This citation reflects the "*nomen abortivum*" approach Sprague (1927) used to define the early misapplications, which, before the Cambridge Congress of 1930, were not considered as sufficient grounds for rejecting a name as a later homonym (Lawrence, 1951), thus allowing an "*emendatum*", or redefinition, as noted by Maire. Maire (1963) went one step further in noting *Tunica* as a *nomen conservandum*. Janchen (1965) argued for conservation of *Tunica* as defined by Mertens and Koch, suggesting that *Petrorhagia* is a superfluous name. I have seen no evidence to indicate that any proposal to conserve *Tunica* has ever been formally presented.

Another name suggested for plants placed in *Tunica* is *Imperatia*, published by Moench (1794) to include one species, *Imperatia filiformis* (= *Gypsophila saxifraga*). Degen (1937) noted *Imperatia* was the correct name for all *Tunica* species except those in section *Koblauschia*. However, as Dandy (1957) noted, this name cannot be used since it is a later homonym of *Imperata* Cirillo, a genus in the Gramineae published in 1792 (Farr et al., 1979).

Petrorhagia was established as a genus of four species by Link (1831), based implicitly on *Gypsophila* section *Petrorhagia* as recognized by Seringe in 1824 (Ball & Heywood, 1964). Dandy (1957) considered this derivation to be a good reason to consider *Petrorhagia* as a synonym of *Gypsophila*, and suggests that the proper name for the genus is *Koblauschia*, a name published by Kunth (1838) for separating two species from *Dianthus*. Dandy's argument and choice of *Gypsophila glomerata* Pallas ex M. Bieb. as lectotype of the genus were rejected by Ball and Heywood (1964). They supported Britton's (1913) choice of *P. saxifraga* as lectotype of *Petrorhagia*, citing the bract condition present in *P. saxifraga* more closely fits Seringe's description than *G. glomerata* and noting that *Petrorhagia* is the Greek word for "saxifraga." I agree with the argument of Ball and Heywood and propose the lectotype as *P. saxifraga* (*vide* Ball & Heywood, Bull. Brit. Mus. (Nat. Hist.), Bot. 3:130. 1964). Dandy (1957) did not specifically mention Britton's lectotypification, giving no indication he was intentionally superseding Britton. Ball and Heywood's action also means that the Britton lectotypification cannot be superseded on the grounds that it is based solely on a largely mechanical method (see Article 8, International Code; Voss et al., 1983).

Some authors, including Holub et al. (1972), still consider *Koblauschia* as a distinct genus of five species. Ball and Heywood (1964) indicated the

three character states usually used to separate *Kohlruschia* from *Petrorhagia*, namely the annual habit, a capitulate inflorescence, and petals possessing a distinct claw and limb, are found in some *Petrorhagia* species outside of their section *Kohlruschia*. Evidence presented by Schaper (1936) illustrates a great degree of ultrastructural similarity in the seeds of *P. prolifera* and *P. saxifraga*, species that would be in different genera if *Kohlruschia* is recognized.

TAXONOMIC CRITERIA

Petrorhagia is a difficult genus to characterize morphologically since variability which can include the predominant states found in both *Dianthus* and *Gypsophila* is present in some characters (e.g., presence/absence of "epicalyx" bracts, petal structure). *Petrorhagia* can be defined as having a combination of seed characters found in *Dianthus* (a straight embryo in the center of a dorsiventrally compressed seed as in Figs. 1 and 2) and calyx characters found in *Gypsophila* (few veins per sepal and scarious commissures separating adjacent sepals). The separation of *Petrorhagia* from *Gypsophila* is a bit more distinct than the boundary between *Dianthus* and *Petrorhagia*. As Ball and Heywood (1964) noted, the seed offers a constant feature that clearly aligns *Petrorhagia* with *Dianthus* and *Velezia*. Pollen data presented by Candau (1980) suggest a similar alignment; pollen shape differences existed between species of *Dianthus* and *Petrorhagia*, while pollen of *Petrorhagia* and *Gypsophila* species differed in both grain size and aperture number. On the other hand, calyx characteristics offer a clear separation between most species of *Petrorhagia* and *Dianthus*, except for two species of section *Dianthella* which possess calyces that approach a *Dianthus* condition, having more veins per sepal and almost lacking scarious commissures between adjacent sepals.

A similar situation exists at the species level, with some very evident characters having little if any diagnostic value. The best example of this situation involves *Petrorhagia velutina* (Guss.) P. Ball & Heyw., a species introduced into California, Oklahoma, and Texas. Most plants of this species, such as those in California, show obvious glandular pubescence on the middle internodes of the stem, illustrating the "velvety" nature implied by the epithet *velutina* (Smith, 1972). The stems of plants collected in Oklahoma and Texas are almost always glabrous, a condition Ball (in Tutin et al., 1964) indicated as occurring in some native populations, especially in Italy. Other morphological characters, such as sheath length, petal venation, and seed surface morphology, are very similar on plants from both areas, showing the fallability of pubescence as a diagnostic character.

The size and surface morphology of the seeds are often very useful features in distinguishing species of *Petrorhagia*, including those found in North America (Figs. 3–6). Three of our taxa, *P. prolifera*, *P. nanteuillii*, and *P. velutina* are very closely related, with *P. nanteuillii* probably derived from hybridization of *P. prolifera* and *P. velutina* sometime in the past. Inspection of the dorsal seed surfaces of these taxa offers a constant character for distinguishing them, with seeds of *P. nanteuillii* (Fig. 5) possessing the basic size and shape of *P. prolifera* (Fig. 4) and a tuberculate surface approaching that of *P. velutina* (Fig. 6).

Other morphological features are correlated with the seed characters to allow positive identification of collections in the absence of seed; these features are noted in the key and descriptions wherever possible. One apparently overlooked character useful in analyzing North American collections is the presence and pattern of darkened petal veins in three of our four species (Figs. 7–10). This character offers another feature that can be used to distinguish members of the *P. prolifera* "complex." Petals of *P. prolifera* (Fig. 8) are uniformly colored; darkened stripes are absent. Petals of *P. nanteuillii* (Fig. 9) that were examined possessed one prominent dark pink stripe on the central vein, while a very faint dark area may be present on the two veins adjacent to the central vein. At least three dark stripes were evident on *P. velutina* petals (Fig. 10) with five or more stripes occasionally present. A similar pattern of petal vein coloration on European specimens of these taxa was noted.

TAXONOMIC TREATMENT

The material presented below deals with the delimitation of the genus as it appears in North America. Synonymy present in Ball and Heywood (1964) will not be repeated here except in cases where usage in this paper or North American references warrant it. Several additional binominals noted during the study will be presented to supplement Ball and Heywood's listings. Abbreviations for major works are taken from Stafleu and Cowan (1976, 1979, 1981, 1983) where possible, with additional abbreviations taken from Tutin et al. (1976, 1980)

PETRORHAGIA (Ser. in DC.) Link, Handbuch 2:235. 1831.

Imperatia Moench, Methodus. 60. 1794.

non *Imperata* Cirillo, Pl. Rar. Neapol. 2: xxvi, t. 11. 1792.

Gypsophila sect. *Petrorhagia* Ser. in DC., Prodr. 1:354. 1824.

Tunica sensu Mert. & Koch in Röhling, Deutschl. Fl. ed. 3. 3:182. 1831.

non *Tunica* Ludw., Inst. Regn. Veg. ed. 2. 129. 1757,

non *Tunica* Boehmer in Ludw., Def. Gen. Pl. ed. 3. 298. 1760,

non *Tunica* Adans., Fam. Pl. 2:255. 1763,

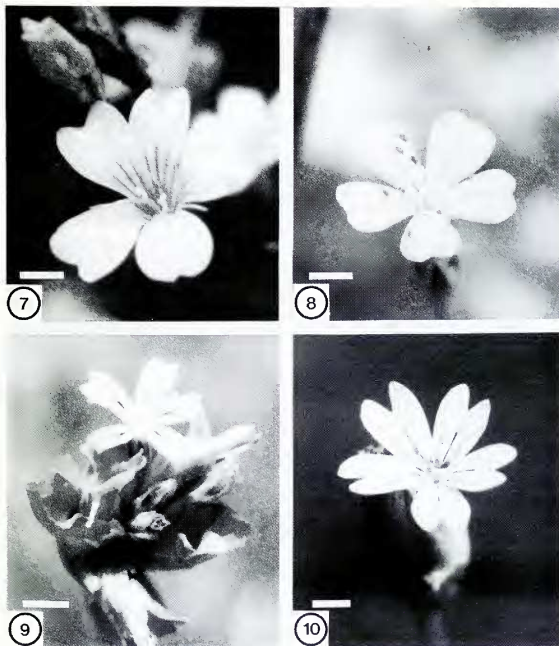
non *Tunica* Scop., Fl. Carn. ed. 2. 1:298. 1772.

Koblerauschia Kunth, Fl. Berol. 1:108. 1838.

Koltrauschia Kunth ex Fourr., Ann. Soc. Linn. Lyon sér. 2. 16:345. 1868. *orth. var.*

Petroragia Link ex Kuntze, Lex. Gen. Phan. 427. 1903. *orth. var.*

Annual or perennial herbs. Stem internodes pubescent or glabrous, pubescence glandular or not. Leaves simple, opposite, linear to narrowly



FIGS. 7-10. Flowers of *Petroragia* spp. Scale = 2 mm. 7. *P. saxifraga*, Canfield Lake, Michigan. 8. *P. prolifera*, Grand Haven, Michigan. 9. *P. nanteuillii*, N of Cazadero, California. 10. *P. velutina*, S of Athens, Texas.

lanceolate, usually 1- or 3-veined, margin often basally scabrous or ciliate; sheath of variable length, often 1–3 times as long as broad. Inflorescence basically a dichasial cyme, bracteate or not, with flowers solitary, fasciculate, paniculate, or capitate (ours solitary or capitate). An “epicalyx” of bracts directly subtending the calyx present (ours) or absent; when present, 1–3 pairs evident. Sepals 5, fused, each 1–3 (rarely 5–7) veined, a veinless commissure separating adjacent sepals. Petals 5, clawed (ours) or not; often pink or white; apex entire to bifid; primary veins 1–3 per petal, with or without contrasting color stripes on veins of the limb. Stamens 10, anthers of ours often pink, blue, or white. Styles 2, can be stigmatic along entire length. Capsule oblong, 4-lobed, dehiscent by 4 apical teeth. Seeds dorsiventrally compressed with facial hilum and straight, central embryo; reddish-brown (immature) to blackish-brown (mature); size variable. Pollen oblate-spheroidal, porate; tectum bearing small spines (Candau, 1980). $X = 13$ and 15 (Favarger, 1966).

TYPE: *Petrorhagia saxifraga* (L.) Link, *vide* Ball and Heywood (Bull. Brit. Mus. (Nat. Hist.), Bot. 3:130. 1964.).

KEY TO PETRORHAGIA AND THREE RELATED GENERA IN NORTH AMERICA

- 1 Bracts subtending the calyx present
 - 2 Commissures (veinless scarious areas) present between adjacent sepals, 1–3 veins per sepal *Petrorhagia*
 - 2 Commissures absent, 5 or more veins per sepal *Dianthus*
- 1 Bracts subtending the calyx absent
 - 3 Commissures present between adjacent sepals, seed laterally compressed with curved embryo *Gypsophila*
 - 3 Commissures absent, seed dorsiventrally compressed with straight embryo *Velezia*

The “epicalyx”, although more evident than calyx commissures, is not completely diagnostic for *Petrorhagia* since 14 of 29 species do not possess subtending bracts. A key, such as that in *Flora Europaea* (Walters in Tutin et al., 1964), using calyx commissures as the first character is appropriate for separating all *Petrorhagia* species from related genera.

KEY TO SPECIES OF PETRORHAGIA IN NORTH AMERICA

- 1 Flowers solitary, or rarely in fascicles of 2–3 (a few cultivars); subtending bracts narrow and short, enclosing to \pm one-half the calyx 1. *P. saxifraga*
- 1 Flowers borne in capitate inflorescence (solitary in some very young plants); bracts of the inflorescence very broad and long, enclosing entire calyx of most flowers
 - 2 Leaf sheath about as long as broad, 1–2 (rarely 3) mm long; petals truncate or emarginate, no dark colored areas on vein of petal limb 2. *P. prolifera*

- 2 Leaf sheath 1.5 – 3 times as long as broad, usually 3 mm or longer; perals obcordate to bifid, 1 – 3 (or more) dark areas present on veins of limb
- 3 Leaf sheath (2)3 – 4 mm long; inner inflorescence bracts obtuse or mucronate; 2 of 3 dark veins of petal limb often faint; seeds (1.3) 1.5 – 1.8 mm long, tuberculate 3. *P. nanteuilii*
- 3 Leaf sheath variable in length, (3)4 – 6(9) mm long; all inflorescence bracts mucronate; 3 (or more) dark areas on veins of petal limb; seeds 1.0 – 1.3(1.4) mm long, covered with conical papillae 4. *P. velutina*

1. PETRORHAGIA SAXIFRAGA (L.) Link, Handbuch 2:235. 1831.

- Dianthus saxifragus* L., Sp. Pl. 1:413. 1753. *Gypsophila saxifraga* (L.) L., Syst. Nar. ed. 10. 2:1028. 1759. *Tunica saxifraga* (L.) Scop., Fl. Carn. ed. 2. 1:300. 1772. *Silene tunica* E. H. Krause in Sturm, Deutschl. Fl. ed. 2. 5:107. 1901. *Imperatia saxifraga* (L.) Degen, Fl. Veleb. 2:94. 1937. *Kohlrauschia saxifraga* (L.) Dandy, Watsonia 4:42. 1957. TYPE: not seen. LINN 579.25 (photo at FI; microfiche at US!) is authentic material. See Savage (1945) for explanation of penned names of 579.24 and 579.25. Described from Switzerland, France, and Germany.
- Gypsophila scabra* Schultes ex Steudel, Nomencl. Bot. ed. 1. 386. 1821. *Tunica saxifraga* var. *scabra* (Steudel) Schur, Oesterr. Bot. Z. 19:16. 1869. Original material not seen.
- Gypsophila permixta* Guss., Suppl. Fl. Sic. Prodr. 120. 1832. *Tunica permixta* (Guss.) E. & A. Huet in Hohen., Bot. Zeitung (Leipzig) 16:295. 1856. *Tunica saxifraga* var. *permixta* (Guss.) Nicotra, Prodr. Fl. Messan. 122. 1883. TYPE LOCALITY: SICILY, original material not seen (NAP?).
- Gypsophila arenicola* Dufour, Bull. Soc. Bot. France 7:240. 1860. *Tunica arenicola* (Dufour) Nyman, Consp. Fl. Eur. 100. 1878. TYPE LOCALITY: SPAIN; "frequens in arena maritima valentina (Dehesa)", original material not seen.
- Gypsophila rigida* Sibth. & Smirh, Fl. Graeca IV. p. 75, t. 382. 1823, non L., fide Gürke in Richter (1903) and Degen (1937). *Imperatia bithynica* Degen, Fl. Veleb. 2: 95. 1937. TYPE LOCALITY: TURKEY, Olympus Bithynus, original material not seen.

Perennial, sometimes woody at base. Stems much branched near the base, 5 to 40 cm [to 45 cm in Ball and Heywood (1964)] tall; internodes glabrous above, scabrous below. Leaves linear, 5 – 20(30) mm long, 1(2) mm or less wide, 1-veined, margin basally ciliate; leaf sheath 1 mm or less long, about as long as broad. Flowers solitary (fasciculate in some cultivars and var. *glomerata*), terminal, 10 mm or less long, on long peduncles. Subtending bracts 2(4), ovate, membranous, mucronate, 1-veined, enveloping up to one-half of the calyx. Sepals 1-veined, margin often ciliate. Petals clawed, limb white to pink, claw often white; primary veins 3 per petal, often dark pink near base of limb; apex obcordate. Anthers pink or white. Seeds with tuberculate surface, (0.8)1.0 – 1.2(1.3) mm long, 0.5 – 0.8(1.0) mm broad. $2n = 30, 60$ (Favarger, 1966). Figs. 3, 7, and 11.

All North American collections I have seen are referable to *P. saxifraga* var. *saxifraga*. Variation within var. *saxifraga* is formally recognized in a

few works [Soó (1970) listed six forms and a "variant"], although it is dismissed by Ball and Heywood (1964) as being of questionable significance. Cultivars, for the most part, are not significantly different from naturalized collections, although some "modifications", such as doubled petals, do occur.

Schlesing and Iltis (1962) cited two common names for this plant; Tunic Flower and Coat Flower, both names referring to the bracts surrounding the flower. Britton (1913) listed Saxifrage Pink and Tunica as common names. A translation of the binomial reveals that both parts are derived from words meaning "rockbreaking", *Petrorhagia* from Greek, *saxifraga* from Latin, alluding to its prevalence in rock crevices (Smith, 1972).

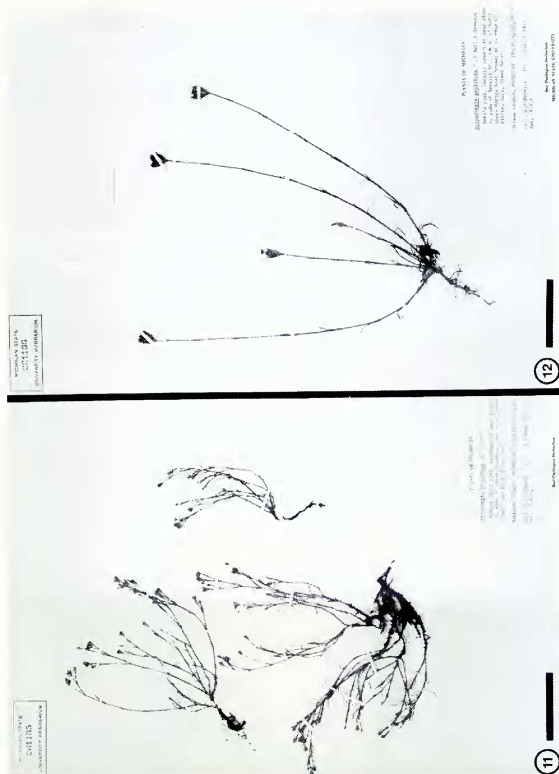
FLORAL BIOLOGY: Meusel and Muhlberg (1979) reported that *P. saxifraga* is strongly protandrous and suggested that self-pollination is hardly possible. Knuth (1908) noted that the style usually matures late enough to prevent selfing. The flowers produce abundant nectar and are visited mainly by small bees, flies, and butterflies (Meusel and Muhlberg, 1979).

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) summarized the native range as "Central and southern Europe and south-western Asia", with naturalized introductions noted for Sweden and Great Britain.

Within North America, most records represent either obvious cultivations or adventive populations (see Fig. 13). From label data, it is clear that many collections were made along roadsides, often from dry sandy areas, while others represent plants in lawns, waste areas, field edges, sandy forest slopes, a lake edge, and gravelly banks. Flowering reported from June to October, the last flowering possibly limited by first autumn frost.

HISTORY OF INTRODUCTION: *Petrorhagia saxifraga* appeared in North America just over 100 years ago, with initial collections being made along roadsides at College Point and Flushing (Queens Co.), New York (*Schrenk* in 1876, AC, CU). According to a note on the AC specimen, the populations remained "well established" there through 1879. The next collections seen were made at London, Ontario in 1886 and 1887, cited by the collectors (*Burgess* in 1886, CAN, GH; *Dearness* in 1886 and 1887, MTMG) as introduced and spreading in gardens, waste places, and roadsides.

A look at popular manuals will reveal that these sites are often the only ones listed for *P. saxifraga*, a practice started by Robinson (1897) and Britton (1897) and continued by Maguire (1950, 1952). Robinson and Fernald (1908) listed these sites in the 7th edition of Gray's Manual, but Fernald (1950) omitted them from the 8th edition along with any mention of the genus or the species! After studying extant collections, it is readily



FIGS. 11–12. Representative herbarium specimens of *Petrorhagia* spp. Scale = 5 cm.
 11. *P. saxifraga*, Rabeler 313 (MSC). 12. *P. prolifera*, Rabeler 314 (MSC).

apparent that, by 1950, this expression of range was grossly inadequate; *P. saxifraga* had been collected in at least 16 additional states (19 including literature references) and 2 provinces (records of six states and one province are obvious cultivations) by that date!

CURRENT STATUS: The list of specimens cited below includes the earliest and most recent records seen from a given state or province that are not thought to be cultivated.

It appears that the non-cultivated range of the species is much smaller today, with post-1960 collections seen only from only Michigan, Virginia, Wisconsin, and Ontario. In Michigan, *P. saxifraga* has been collected in 10 counties since 1960, almost all specimens representing naturalized populations. It is extremely abundant as a lawn and roadside weed in the Manistee area, where the first collection dates from 1924.

Post-1960 collections of cultivated plants were seen from Massachusetts (*Wiegel and Hodgdon* 12043, NHA), Michigan (*Bourdo* 4056 & 5865, MCTF; *Rabeller* 308, MOR, MSC, NA), Minnesota (*McWilliams* in 1966, NA), and New York (*Stites* in 1978, BH), indicating the potential for growth and possible escape in other areas. Since *P. saxifraga* is available commercially as a landscape plant, it is difficult to predict when or where the next escape may take place, and whether or not an adventive population will result.

Representative specimens: UNITED STATES. IDAHO. KOOTENAI CO.: Sandy lake shore, Coeur d'Alene, Oct 1914, *Rust* 446 (WTU). ILLINOIS. CHAMPAIGN CO.: Roadside, Champaign, 28 Jun 1950, *Elkin* 147 (ILL). COOK CO.: South Park, Jun 1887, *Oblendorf* s.n. (F). MAINE. KNOX CO.: Rockport, 23 Aug 1930, *Steiermark* 4163 (F). MASSACHUSETTS. BRISTOL CO.: Rockery, North Easton, 1 Jul 1916, *Schweinfurth* s.n. (LL). WORCESTER CO.: Dooryard, Leominster, 9 Aug 1943, *Clark* s.n. (NEBC). MICHIGAN. DELTA CO.: Gravel bank fill, Fishdam River, 3 mi E of Isabella, T41N, R18W, S33, SW ¼, 11 Sep 1981, *Rabeller* 670 (FLAS, MIN, MSC, RM, VT); 12 Jul 1982, *Rabeller* 723 (MSC, UTC, VDB); 17 Aug 1982, *Henson* 1436 (MICH). KENT CO.: Grand Rapids, 22 Jun 1899, *Stevenson* s.n. (MICH). MINNESOTA. ST. LOUIS CO.: Wooded slope at Vermillion Dam, 7 Aug 1940, *Lakela* 3992 (DUL, MIN, MO, SMU, UC). NEW JERSEY. CAPE MAY CO.: Roadside, Cold Spring, 12 Aug 1915, *Brown* s.n. (PH); roadside fence-row, Cold Spring, 25 Sep 1920, *Brown* s.n. (PH). NEW YORK. QUEENS CO.: College Point, 1876, *Schrenk* s.n. (AC); Flushing, L. I., 1876, *Schrenk* s.n. (CU). TOMPKINS CO.: Lawn weed, Cornell Heights, Ithaca, 17 Jul 1940, *Eames*, *Flora of New York* 20162 (CU). PENNSYLVANIA. MONTGOMERY CO.: Pennsburg, 28 Jun 1919, *Brendle* s.n. (PH). SOUTH DAKOTA. LAWRENCE CO.: Glade on talus slope, alt. 3900 ft, 11 Aug 1942, *Bennett* 1521 (MO). VIRGINIA. PAGE CO.: Old homesite, Skyland, 4 Jul 1965, *Mazzeo* 1084 (NA); 25 Sep 1966, *Mazzeo* 1781 (NA). WISCONSIN. COLUMBIA CO.: Outskirts of a cornfield and roadside, Okee, T10N, R8E, S7, 29 Sep 1967, *Domres* s.n. (WIS). SHEBOYGAN CO.: Roadside, Sheboygan, Aug 1912, *Goessl* s.n. (WIS).

CANADA. BRITISH COLUMBIA. Prince George, Sep 1937, *Travis* s.n. (DAO). ONTARIO. MIDDLESEX CO.: Gardens and waste places, London, Sep 1886, *Burgess* s.n. (CAN).

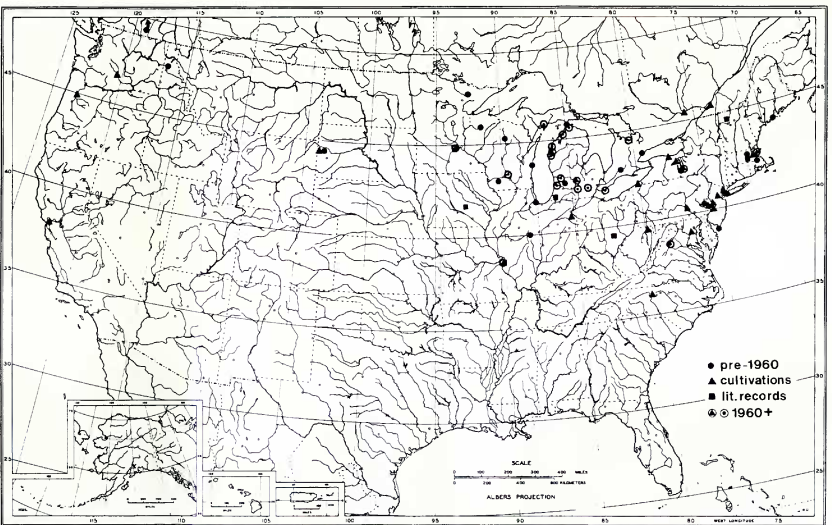


FIG. 13. North American distribution of *Peromphaga saxifraga*.

SIMCOE CO.: Waste soil near grain elevator, Collingwood, 9 Sep 1978, A. A. and S. A. Reznicek 4866 (MICH, [TRT]).

Records mapped from literature (specimens not seen): IOWA. Grinnell(?) (Conard, 1943). MASSACHUSETTS. Worcester (Potter & Woodward, 1935). MICHIGAN. Niles (Beal, 1908). OHIO. Hocking County in 1930 (Cusick & Silberhorn, 1977). VERMONT. Morrisville (Dole, 1937).

Literature records rejected: DISTRICT OF COLUMBIA. Brookland (McAtee, 1940; Hermann, 1946). This record is based on a misidentified collection of *Gypsophila muralis* (Ulke s.n., without date, US).

2. PETRORHAGIA PROLIFERA (L.) P. Ball & Heyw., Bull. Brit. Mus (Nat. Hist.), Bot. 3:161. 1964.

Dianthus prolifer L., Sp. Pl. 1:410. 1753, nec Forsskål, Fl. Aegypt. — Arab. xxv. 1775, nec Sibth. & Smith, Fl. Graec. Prodr. 1:285. 1809, *fide* Graebner and Graebner (1921). *Tunica prolifer* (L.) Scop., Fl. Carn. ed. 2. 1:299. 1772. *Koblauschia prolifer* (L.) Kunth, Fl. Berol. 1:109. 1838. *Cylichnanthus prolifer* (L.) Dulac, Fl. Haute-Pyrénées, 261. 1867, *nom. illeg.* *Gypsophila prolifer* (L.) Arcang., Comp. Fl. Ital. ed. 2. 303. 1894. *Silene prolifer* (L.) E. H. Krause in Sturm, Deutschl. Fl. ed. 2. 5:107. 1901. LECTOTYPE (Thomas, 1983): ex Horti Uppsal. (S, microfiche at US!). See Thomas for argument rejecting earlier lectotypification of Ball and Heywood (1962) with LINN 581.7 (photographs at BH!, F!, GH!, NY!). Described from Germany and southern Europe.

Dianthus diminutus L., Sp. Pl. ed. 2. 1:587. 1762. *Caryophyllus diminutus* (L.) Christm., Vollst. Pflanzensyst. 6:563. 1780, *fide* Merrill (1938), *nom. illeg.* *Koblauschia diminutus* (L.) Reichb., Icon. Fl. Germ. Helv. 6:43, t. 247, f. 5008. 1844. TYPE: not seen. Described from Germany.

Dianthus carolinianus sensu Torrey & A. Gray, Fl. N. Amer. 1(2):195. 1838, non Walter. TYPE: from South Carolina, Walter (?) (BM, photo at A!).

Annual. Stems simple or branched near the base, (6) 11–60 (commonly 30) cm tall; internodes mostly glabrous, middle internodes may be slightly scabrous. Leaves linear to linear-oblong, 10 mm long, 2(3) mm or less wide, 3-veined, margin scabrous; leaf sheath 1–2 (rarely 3) mm long, as long as broad, or at lower nodes, often broader than long. Inflorescence capitate (occasionally reduced to one flower), 10 mm or more long, usually 5–20 mm broad. Subtending bracts broadly ovate, brown-scarious, many veined, enclosing the flowers; tips of bracts obtuse, or outermost may be mucronate. Sepals 3-veined, outer surface not scabrous, margin glabrous. Petals clawed, pink or slightly purplish (rarely white); primary veins 1 per petal, dark coloration near base of limb absent; apex truncate or emarginate. Anthers pink or blue; pollen 40 μ m in diameter, apertures of 4 μ m (Candau, 1980). Seeds with fine to coarse reticulate surface, (1.1) 1.3–1.6(1.8) mm long, (0.7)0.8–1.0(1.1) mm broad. $2n = 30$ (Ball & Heywood, 1962; Thomas & Murray, 1983). Figs. 1, 2, 4, 8, and 12.

Variance shown in the above characters is, for the most part, distributed throughout the range, although slightly scabrous internodes and finely reticulate seeds are more prevalent in plants from New Jersey, Pennsylvania, and Virginia. I agree with Ball and Heywood (1964) in not applying subspecific categories, such as those used by Briquet (1910) and Maire (1963) to describe leaf margin texture variation, or the seven forms and two "variants" listed by Soó (1970), to segregate minor variants within *P. prolifera*.

Britton (1913) gave three common names for *P. prolifera*; Proliferous Pink, Childing Pink, and Childing Sweet William. Smith (1972) defined the epithet "prolifera" as: "Proliferous, i.e. free flowering or producing side shoots or buds in order to increase." This is an appropriate description of the plant and "proliferous" can be extended to include the relatively large quantity of seed produced by each plant.

FLORAL BIOLOGY: Thomas and Murray (1981) described two "races" of *P. prolifera* after finding selfing and outcrossing populations that were reproductively isolated from each other. Subsequently, Thomas (1983) treated the large-flowered outcrossing plants as a separate "sister" species (*P. obcordata*), leaving *P. prolifera* as having small, autogamous flowers that produce little nectar and are homogamous, or as in one of their study populations, protandrous. I have observed distinctly protandrous flowers with protruding stamens and (later) style branches at Grand Haven, Michigan, suggesting that some outcrossing may take place from chance insect visits.

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) stated the native distribution as "Central Europe, mountains of southern Europe, Caucasus, Turkey (northern Anatolia), mountains of western North Africa", with introductions noted in Great Britain.

Nearly all collections of *P. prolifera* within North America are from the southeastern portion of the continent (see Fig. 14), most being gathered from roadside localities, either in sand, gravel, or shale fill. Dry fields and pastures are mentioned as collection sites from Pennsylvania to North Carolina, while seven Virginia collections are of plants found growing in cinder railroad ballast. The calcareous soils of the Ozark region may be a factor in the spread of *P. prolifera* away from the roadside and into the glades and pastures in northern Arkansas and southern Missouri. Flowering reported from late May through late September.

HISTORY OF INTRODUCTION: *Petrorhagia prolifera* apparently first appeared in North America near Philadelphia, Pennsylvania shortly after 1800. The earliest specimens seen bear the name *Dianthus carolinianus*, a

name published by Walter (1788) in his *Flora Caroliniana*. A problem develops when one attempts to determine what plant Walter had in mind for *D. carolinianus*. *Index Kewensis* (Hooker & Jackson, 1895) lists *D. carolinianus* as a synonym of *Dianthus armeria* L. Asa Gray inspected Walter's herbarium in 1839 (at the time in possession of John Fraser in England) and wrote "his '*Dianthus carolinianus*' is *Frasera*! in fruit." (Britten, 1921). In his monograph of *Dianthus*, Williams (1893) considered *D. carolinianus* a synonym of *Dodecatheon meadia* L. Britten (1921) reached the same conclusion when he investigated Walter's herbarium, stating "but the *Dianthus* is not *Frasera*, but *Dodecatheon meadia*." A translation of Walter's description of *D. caroliniana* is not of much help: "with flowers clustered on long peduncles, tube scales smaller by one-half." (Walter, 1788), characteristics which could apply to fruiting material of all of the above-mentioned taxa! An inspection of the set of photographs of Walter's herbarium at A (Schubert, 1946-47) revealed a small specimen in the upper left corner of page 40 inserted in a small piece of paper labeled "334 *Dianthus carolin.*" It is indeed *Dodecatheon meadia*, consisting of several erect capsules and attached calyces and a 7.5 cm section of the scape.

Torrey and Gray (1838) listed *D. carolinianus*, citing South Carolina for its range and add the following note: "*D. prolifer* was sometime since cultivated at Bartram's garden under this name", connecting the name to early collections from the Philadelphia area. The actual dates of cultivation of *P. prolifera* at Bartram's garden remain a mystery. John Bartram started a seed exchange with a number of European botanists in the late 1730's, trading native American plants for those of Europe for cultivation in his garden. This activity continued into the 1830's under the guidance of Bartram's children after his death in 1777 (Berkeley & Berkeley, 1982) and would provide a logical explanation of the appearance of *P. prolifera*. The earliest evidence of its cultivation is the specimen at PH collected by S. W. Conrad labeled "*Dianthus carolinianus* Walter. At, and in the vicinity of Bartram's Garden." This collection would have been made prior to 1815 based on details of Conrad's life and his use of Linnaean classification (Decandria Digynia) on the label (Harshberger, 1899).

The earliest dated collection seen was that of E. M. Durand (*Durand* in 1837, GH) on which he noted: "It seems to be perfectly naturalized on that spot [a rock near the garden] and is not found in the garden itself." On both this specimen and an undated collection from South Carolina (*Durand*, NY), Durand questioned his determination of *D. carolinianus*, with the South Carolina specimen labeled: "*D. prolifer* of Europe and believe it to be the same, introduced." The site of the first naturalized population referred to by Durand is most likely the same one that at least 10 collectors visited in



FIG. 14. North American distribution of *Peromyscus polifera*.

the next 60 years; a hill, described as "dry, micaceous-sand" (C. E. Smith, NY), along the Schuylkill River, near Bartram's garden and Gray's Ferry. It is not known how long this population existed, but the most recent collection seen was dated 21 October 1891 (Crawford, PH).

Other pre-1900 collections exist for Delaware (1896-97), Maryland (1887), New Jersey (1871), New York (Britton, 1879, specimens at SIM?), and Ohio (1891-96).

CURRENT STATUS: The specimens cited below include the earliest and most recent records seen from a given state excluding collections of cultivated material. The distribution of post-1960 collections (Fig. 14) is far different from that listed by major manuals. Fernald (1950) stated "sandy fields and roadsides, local, s. N.Y. to Del., Va., Ky. and O.", which, except for the Ohio reference, corresponds to the distribution of pre-1949 specimens present in the loan received from GH for this study. Maguire (1952) considered *T. prolifera* "sparingly introduced in waste places, N.Y. to S.C. and Cal." This description nearly matches the pre-1952 specimens seen from NY, the institution Maguire was associated with at that time (the California specimens at NY are *P. velutina*, although labeled *T. prolifera*; one Idaho collection (cultivated?) labeled *D. armeria*, one Ohio collection not mentioned). Both treatments generalize the distribution by inserting "to" and thus connecting widely separated local populations, making the species seem more widespread than it may actually be. The reader is referred to three similar situations recorded elsewhere (Shinners, 1965; Shinners, 1969; Rabeler, 1981) which treat discontinuities between current ranges and those given in the literature.

In light of the discrepancies noted, a few general conclusions are in order. Several states should be dropped from previously published ranges; California (the origin of the Congdon collection (1902) remains a mystery), Ohio (last collected there in 1896), South Carolina (record relies on Durand collection of early 1800's), and Texas, as listed by Shinners (1969) and Correll and Johnston (1970), since all Texas collections are in fact *P. velutina*. Several areas might be retained, since populations could exist there in spite of available records; Delaware (last collected there in 1897, but present in all neighboring states; see Phillips (1978) for opposing view), Kentucky (single record in Braun (1943) based on a 1941 collection), New York (several collections on Long Island, 1920-48), North Carolina (1949 collection mapped in Radford et al. (1965), but not discussed by the collectors in their report on additions to the flora of North Carolina found in 1949 and early 1950 (Fox, Godfrey, & Blomquist, 1950), or in Radford et al. (1968)), and West Virginia (single report by Core (1941), but Monroe

Co. is close to "active" Virginia populations).

Post-1960 records define a pattern of scattered, local populations from New Jersey southwestward into Virginia and then generally westward into Arkansas and Oklahoma, along with disjunct populations in western Michigan [discussed in more detail in Rabeler (1980)]. The southwestward expansion has taken place for the most part since 1930, with an invasion into the westernmost states occurring since 1950. The irregular timing of appearance in adjacent states makes a theory of multiple introduction into the southeast far more plausible than trying to derive all these populations from the initial introduction in Philadelphia.

Several collections seen indicated that *P. prolifera* has been present at some sites for over 30 years, suggesting naturalization has taken place in areas of Maryland, Pennsylvania, and Virginia. The absence of *P. prolifera* from a recent survey of roadside vegetation at selected sites in southwestern Virginia (Schmaltz, 1981) reinforces the local distribution of *P. prolifera*, even in the vicinity of naturalized populations, since it has been reported at least once in five of the seven counties included in the study. Other post-1960 collections represent adventive occurrences, especially records in three states (Georgia, Michigan, and Tennessee) where the earliest specimen seen was collected after 1975.

How then does *P. prolifera* get around? Soó (1970) listed anemochory, endozoochory, and autochory as dispersal mechanisms of *P. prolifera* in Hungary. *Petrorhagia prolifera*, as well as *P. nanteuilii* and *P. velutina*, would be defined by Van der Pijl (1982) as wind-ballists, with seeds falling from the capsules as the long, wiry stems sway in the wind; a combination of anemochory and autochory would be ideal in open areas such as road shoulders. Ridley (1930) reported Dymes has found that one of the common seeds in an ant grainery in Italy was *P. saxifraga*; similarities between the seeds of *P. saxifraga* and the above-mentioned species suggest that harvester ants may be responsible for occasional short distance dispersal events.

The presence of "roadside" on a large number of labels suggests that occurrences of *P. prolifera* may be partially "transportation-related". Frenkel (1970), in a study of roadside vegetation in California, listed several attributes present in many roadside plants, some of which apply to *P. prolifera*: annual habit; small, light, non-appendaged seeds produced in abundance; and tolerance of high light intensity. Wofford et al. (1977) suggested that *P. prolifera* has appeared in Tennessee as a contaminant of grass seed planted along Interstate 40; contaminated seed is likely responsible for the appearance of *P. velutina* in Texas (Shinners, 1969; Correll & Johnston, 1970) and possibly some of the plants in Michigan (Rabeler, 1980). This situation may easily have occurred in other areas along the

recently constructed interstate highways of the region, a system primarily built since 1960.

Some roadside populations of *P. prolifera* may be unintentionally enlarged if the shoulder area is mowed in mid-summer, since plants would have open capsules of seed awaiting dispersal. This notion became evident after observing a tremendous increase in both number of plants and the area they occupied along an infrequently mowed Michigan roadside 5 years after discovering the population, an increase that I find hard to explain if only "natural" dispersal is invoked.

Representative specimens: UNITED STATES. ALABAMA. FRANKLIN CO.: Roadside, Co. 79, 1 mi N of AL 24 jct., Russellville, 28 May 1967, *Baskin, Caudle, and Turner* 582 (VDB); Roadside, Co. 83, 0.8 mi N of AL 24 jct., E of Russellville, 5 Jun 1981, *Godfrey, Gholson, and Webb* 78789 (FSU). MARION CO.: Sandy clearing by AL 17, N of Hamilton, 20 Jul 1970, *Kral* 40202 (AUA, GH, MICH, MO, OS, SMU, TENN, UNA, US, VDB). ARKANSAS. FULTON CO.: Old pasture near creek, Mammoth Spring, 17 Jun 1951, *Moore* 510472 (UARK); beside US 63 at Trace Creek, T21N, R5W, S4, 4 Jul 1968, *Thomas*, *Bio. (Bot.)* 451 class 10046 (A, CHSC, CM, NCU, NLU(2), NY, SMU, TENN, USF, WTU). WASHINGTON CO.: Along Hwy 71, 6 mi S of Westfork, 8 Jul 1975, *Weeks* 127 (UARK). CALIFORNIA. MARIPOSA CO.: Mariposa Creek, 15 Jun 1902, *Congdon* s.n. (MIN, US). DELAWARE. SUSSEX CO.: Sandy fields and roadsides, S. Milford, 16 Jul 1896, *Commons* s.n. (GH, NYS); road to Slaughter Beach, 12 Aug 1897, *Commons* s.n. (PH). GEORGIA. GREENE CO.: Pasture with granite outcrops, W of Siloam, 5 Jul 1983, *Allison* 1836 (GA). ROCKDALE CO.: Roadside granitic flatrock, Conyers, 28 Jul 1983, *Allison* 1845 (GA). IDAHO. BONNER CO.: Gravel slope, Sandpoint Substation, 11 Sep 1932, *Christ* 2093 (NY). KENTUCKY. ROBERTSON CO.: Roadside, Kentonville [Kenton town?], 8 Jul 1941, *Braun* 4041 (GH, US). MARYLAND. CALVERT CO.: Sandy roadside fill, 1.2 mi S of Bowens, 13 Jun 1981, *Rabaler* 578 (FLAS, MARY, MSC). KENT CO.: Sandy fields near Millington, 18 Jun 1887, *Brinton* s.n. (PENN, PH). MICHIGAN. MUSKEGON CO.: Beside paved area, main entrance, P. J. Hoffmaster State Park, 18 Jul 1983, *Wells and Thompson* 83221 ([BLH], MSC). OTTAWA CO.: Kitchel Dune, Grand Haven, 8 Aug 1976, *Atwood, Beaman, and Rabaler* 409 (MSC); sandy roadside, S edge of Kitchel Dune, [Nature Conservancy Preserve] T8N, R16W, S20, SW 1/4, 9 Aug 1979, *Rabaler* 314 (CAN, DAO, GA, HSC, MICH, MSC, NY, SMU, WAT). MISSOURI. GREENE CO.: Open limestone barrens, Kissick, T28N, R21W, S19, 6 Jun 1982, *Summers* 1025 (MO). STONE CO.: Rocky places near pasture, 5.5 mi SE of Shell Knob, T22N, R24W, NE sect. 18, NW sect. 17, 13 Jul 1956, *Steyermark* 81924 (F, GH, ILL, MO, UMO). NEW JERSEY. CAMDEN CO.: Roadside, Haddonfield, 3 Jun 1871, *Parker* s.n. (F, GH, MO, PENN, PH). CUMBERLAND CO.: Fallow fields, NJ 548, near Mauricetown, 31 Jul 1975, *Reed* 98005 (NCU). NEW YORK. SUFFOLK CO.: Dry sand-pit, Southampton, 18 Aug 1920, *St. John* 2878 (CU, GH, NYS, PH, US); Noyack, 16 Sep 1948, *Latham* 28248 (NYS). NORTH CAROLINA. ASHE CO.: Dry hillside pasture, near US 221, N of Laurel Knob Gap, 7 Sep 1949, *Fox and Godfrey* 3368 (GH, NCSC, NY, TENN, US). FORSYTH CO.: Edge of field near Mt. Carmel Church, 19 Jul 1935, *Correll* 2702 (NA). OHIO. CUYAHOGA CO.: Cleveland, May 1891, *Beardslee* s.n. (MICH, NY(2)); Cleveland, 8 Aug 1896, *Stair* s.n. (OS). OKLAHOMA. CHEROKEE CO.: Open roadside, OK 51, 7.2 mi E of Hulbert, 2 Jun 1951, *Wallis* 533 (OKLA); Roadside, OK 10, 4.5 mi NE of Talequah, 30 Jun 1976, *Taylor* 22206 (DUR, NLU). PENNSYLVANIA. BERKS CO.: Roadside, NE of Virginsville, 16 Jul 1965, *Wilkins* 11659 (PENN).

PHILADELPHIA CO.: At, and in vicinity of Bartram's Garden, without date, *Conrad s.n.* (PH); below Bartram's garden, 18 Jul 1837, *Durand s.n.* (GH). SOUTH CAROLINA. CHARLESTON CO.: Vicinity of Charleston, without date, *Durand s.n.* (NY). TENNESSEE. CUMBERLAND CO.: Roadside, E lane of I-40, near mile 313.8, 28 Jun 1976, *Phillippe, Wofford, Webb, Rader, and Smith 51790* (TENN); 13 Jun 1977, *D. H. and B. Webb 971* (TENN). VIRGINIA. BATH CO.: Weedy railroad margin at Copeland, 23 June 1982, *Wieboldt 4359* (VPI). FAUQUIER CO.: In quarry lane S of US 55, 8 Jun 1941, *Allard 8889* (CM, F, GH, MO, NY, US, VPI). MONTGOMERY CO.: Pasture, near Blacksburg, 8 Jun 1930, *Morton 1838* (US).

Records mapped from literature (specimens not seen): MARYLAND. Annapolis (Shreve, 1910). NEW YORK. Staten Island (Britton, 1879). VIRGINIA. Augusta, Bedford, Nelson, Pittsylvania, and Roanoke Counties (Harvill et al., 1981). WEST VIRGINIA. Monroe Co. (Core, 1941).

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Literature record rejected: MICHIGAN. KENT CO.: Grand Rapids (Cole, 1901). This record is based on a misidentified collection of *Petrorhagia saxifraga* (Stevenson in 1899, MICH).

3. *PETRORHAGIA NANTEUILII* (Burnat) P. Ball & Heyw., Bull. Brit. Mus. (Nat. Hist.), Bot. 3:164. 1964.

Dianthus nanteuilii Burnat, Fl. Alpes Marit. 1:221. 1892. *Dianthus prolifer* var. *nanteuilii* (Burnat) Coincy, J. Bot. (Morot) 12:55. 1898. *Tunica nanteuilii* (Burnat) Gürke in K. Richter, Pl. Eur. 2(3):338. 1903. *Tunica prolifera* var. *nanteuilii* (Burnat) Briq., Prodr. Fl. Corse. 1:569. 1910. *Tunica prolifera* subsp. *nanteuilii* (Burnat) Graebner & P. Graebner in Asch. & Graebner, Syn. Mitteleur. Fl. 5(2): 264. 1921. *Koblauschia nanteuilii* (Burnat) P. Ball & Heyw., Watsonia 5:115. 1962. *Koblauschia prolifera* subsp. *nanteuilii* (Burnat) M. Lafínz, Bol. Inst. Estud. Asturianos (Suppl. Ci.) 10:177. 1964. *Petrorhagia prolifera* subsp. *nanteuilii* (Burnat) O. Bolòs & Vigo, Butl. Inst. Catalana Hist. Nat., 38 Bot 1:87. 1974. TYPE: "Description sur 38 éch [antillons]. de diverses localités de Cannes et d'Agay, dus à l'obligeance de M. R. de Nanteuil." Original material not seen (G?).

Koblauschia velutina var. *intermedia* Pérez Lara in Willk. Suppl. Prod. Fl. Hisp. 282. 1893. *Tunica pinetorum* Pérez Lara, Anales Soc. Esp. Hist. Nat. 25:197. 1896. TYPE LOCALITY: SPAIN, Cadiz province. Original material not seen (MAF).

Dianthus prolifer var. *atapuercae* Coincy, J. Bot. (Morot) 12:54. 1898. *Tunica prolifera* var. *atapuercae* (Coincy) Gürke in K. Richter, Pl. Eur. 2(3):338. 1903. TYPE LOCALITY: SPAIN, "Les bords de la grotte jurassique d'Atapuerca près Burgos." (P?). Original material not seen.

Annual. Stems simple or branched near the base, 21–52 (often 30) cm tall; internodes glabrous or lower and center internodes somewhat scabrous with eglandular pubescence. Leaves mostly linear, 3-veined, margin scabrous; leaf sheath mostly (2)3–4 mm long, 1.5 to 2 times as long as broad. Inflorescence capitate as in *P. prolifera*, 10–12 mm long, 9–17 mm broad, but with tips of inner inflorescence bracts either obtuse or mucronate. Sepals 3-veined, outer surface may be very slightly scabrous, margin glabrous. Petals clawed, pink or slightly purplish (limb rarely white);

primary veins 3 per petal, at least the center vein darkly colored at the base of the limb, 2 side veins may show faint darkening; apex obcordate or somewhat bifid. Pollen $46\text{ }\mu\text{m}$ in diameter, apertures of $4.9\text{ }\mu\text{m}$ (Candau, 1980). Seeds tuberculate, (1.3)1.5–1.8 mm long, (0.7)0.9–1.0 mm broad. $2n = 12, 36$ (Borgen, 1974), 60 (Fernandes & Leitão, 1971; Thomas & Murray, 1983). Figs. 5, 9, 15.

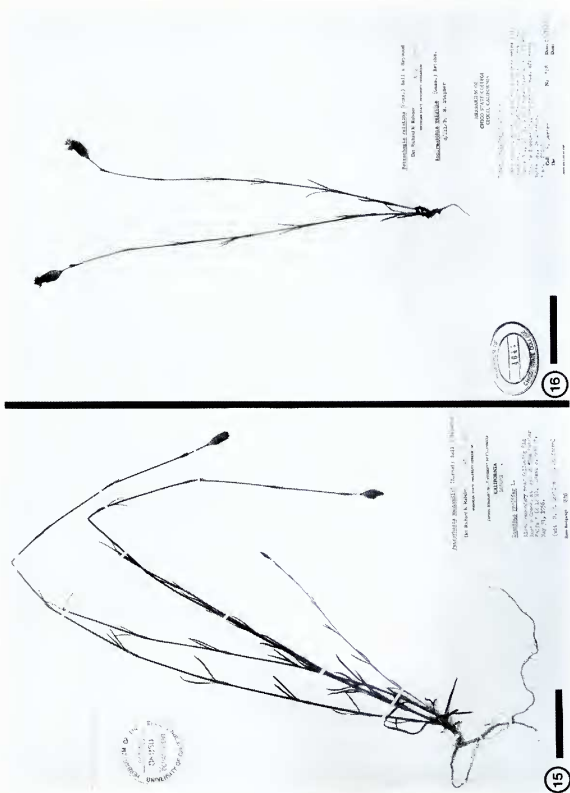
A note on the inclusion of *Tunica pinetorum* Pérez Lara as a synonym of *P. nanteuilii* (Burnat) P. Ball & Heyw. is in order. In his description, Pérez Lara (1896) clearly considered the plant intermediate between *T. prolifera* and *T. velutina* and cited leaf sheath, bract, petal, and seed characteristics that are clearly referable to *P. nanteuilii*. In their catalog of the flora of Cadiz province, Galiano and Silvestre (1977) listed the four collections cited by Pérez Lara after the description of *T. pinetorum* under *P. velutina* without any explanation. The specificity of the description of *T. pinetorum* makes an examination of the specimens crucial before resolution of this discrepancy can be obtained.

Much debate has taken place concerning the status of this plant, as shown by the above list of synonyms. Most chromosome counts of this species indicate a tetraploid condition, with $2n = 60$. The question then arises as to the origin of the tetraploidy; is it an auto- or allopolyploid? Of hybrid or non-hybrid origin?

Böcher et al. (1953) conducted the first investigation of these tetraploids, concluding they represent an autopolyploid race of *Koblranschia prolifera*. In their study, the only clear cut morphological difference cited was seed size, with other characters showing a great deal of overlap between diploid and tetraploid plants. Böcher et al. (1953) used the term "polyplotype" to describe the situation and summarized the problem by stating: "There is greater reason to distinguish the diploid *Koblranschia velutina* from the diploid *K. prolifera* than to distinguish the polyplotypes within the latter." This idea roughly parallels the taxonomy most recently expressed by Bolòs and Vigo (1974). In considering *P. nanteuilii* as a subspecies of *P. prolifera*, they believed *P. nanteuilii* to be a race of *P. prolifera* that has not attained a degree of difference great enough to warrant treatment as a distinct species.

Ball and Heywood (1962) first suggested the alternative view; an allotetraploid with *K. prolifera* and *K. velutina* as parents. Their position was based on the presence of characteristics, including flowering time and seed surface texture, that are intermediate between the two species. They noted this heritage would be shown in the karyotype by the presence of a pair of very short chromosomes present only in *K. velutina*.

As part of their study on the breeding systems in *Petrorhagia* sect. *Koblranschia*, Thomas and Murray (1983) conducted a cytological investiga-



FIGS. 15 – 16. Representative herbarium specimens of *Petrorhagia* spp. Scale = 5 cm.
 15. *P. nanteuilii*, Bacigalupi, Robbins, & Hoffman 5676 (DAV). 16. *P. velutina*, Carter 368 (CHSC).

tion of *P. nanteuillii*. They noted the presence of 29 pairs of metacentric chromosomes and one pair of small telocentric chromosomes, reinforcing the contention of Ball and Heywood (1962), and found that *P. nanteuillii* behaved as an allotetraploid during meiosis, with strictly bivalent pairing. They suggested one genome was supplied by *P. prolifera* [based in part on homeologous pairing in artificial sterile hybrids noted earlier by Thomas (1980)], the other most likely coming from *P. velutina*, although breeding barriers within *P. velutina* prevented formation of any *P. velutina*-*nanteuillii* hybrids. In addition, Thomas (1980) found that all attempts to cross *P. velutina* with *P. prolifera* were unsuccessful, suggesting that any hybridization that may have led to *P. nanteuillii* would have taken place prior to the development of the breeding barrier now present in *P. velutina*. This is confirmed by the lack of transitional forms between *P. nanteuillii* and the reputed parents, a situation first noted by Nanteuil (Burnat, 1892) and emphasized by Ball and Heywood (1962).

On the basis of the above cytological evidence and observed morphological continuity, I have decided to follow both Ball and Heywood (1964) and Thomas and Murray (1983) in recognizing *P. nanteuillii* as a separate species. Maire (1963) used stem pubescence to recognize two varieties, a useless distinction considering the instability of this character in section *Kobtrauschia*.

The common name Childing Pink is not used only for *P. prolifera*, Perring and Farrell (1977) applying it to *P. nanteuillii*. The epithet "*nanteuillii*" was chosen by Burnat (1892) in commemoration of Edmond Nanteuil, who discovered this species near Cannes, France in 1885.

FLORAL BIOLOGY: Thomas and Murray (1981) reported *P. nanteuillii* to be primarily autogamous, noting that the timing of anthesis and stigma emergence tended to coincide and seed set was high under insect-free conditions. Limited cross-pollination may occur since the stigmas do protrude above the corollas.

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) reported the species from "western Europe and western North Africa" with collections cited from the Channel Islands, Madeira, and the Canary Islands, areas where neither *P. prolifera* nor *P. velutina* have been collected. Two specimens have been seen from Australia (Clemens in 1944 and 1949, MICH), indicating an introduction to Queensland. Perring and Farrell (1977) listed it as endangered in England, citing the small number of localities and their accessibility to the public as reasons to be concerned about its status.

The single California population (Fig. 17) is located among grasses in dry roadside soil, a habitat similar to several of the sites supporting *P. prolifera*

and *P. velutina* in other states. Flowering is reported in late May, with a few plants continuing into early August.

HISTORY OF INTRODUCTION AND CURRENT STATUS: Unfortunately, the early history of *P. nanteuilii* in North America is unknown. Although both species that appear to have contributed to the genome of *P. nanteuilii* have been collected in California (*P. prolifera* only once, about 200 miles southeast of Cazadero), evidence presented by Thomas (1980) and Thomas and Murray (1983) suggests that no such hybridization is currently possible. No evidence of previous cultivation either at or near the roadside site was present, suggesting that *P. nanteuilii* may have arrived as a seed contaminant.

The specimens cited below illustrate the restricted occurrence of *P. nanteuilii* in North America; a single wild population in California known since 1956 and an intentional cultivation at the Bailey Hortorium in 1969. An investigation of seeds and vegetative material from eastern Sonoma County provided by Dr. Charles Quibell revealed no trace of *P. nanteuilii* among the *P. velutina* plants there, suggesting the population may be spreading slowly if at all.

Representative specimens: UNITED STATES. CALIFORNIA. SONOMA CO.: Along secondary road following Big Austin Creek, at base of "The Butcher Knife", elev. c. 600 ft, 31 May 1956, *Bacigalupi, Robbins, and Hoffman* 5676 (DAV, JEPS); along trail to Big Austin Creek, N side of King Ridge Rd., 4.4 mi N of Cazadero, T9N, R11W, "S31", 8 Aug 1980, *Rabaler* 507 (CHSC, GH, HSC, MSC, ROPA, UC, US). NEW YORK. Tompkins Co.: Hortorium Garden, Ithaca, 2 Aug 1969, *Dress* 10606 (BH69-192) (BH).

4. PETRORHAGIA VELUTINA (Guss.) P. Ball & Heyw., Bull. Brit. Mus. (Nat. Hist.), Bot. 3:166. 1964.

- Dianthus velutinus* Guss., Ind. Sem. Boccad. 1825:2. 1825; Pl. Rar. 166, t. 32. 1826.
Tunica velutina (Guss.) Fischer & C. Meyer, Index Sem. Hort. Petrop. 6:66. 1840.
Koblauschia velutina (Guss.) Reichb., Icon. Fl. Germ. Helv. 6:43, t. 247, f. 5010. 1844.
Dianthus prolifer subsp. *velutinus* (Guss.) Battand. in Battand. & Trabut, Fl. Algérie 1:143. 1888.
Dianthus prolifer var. *velutinus* (Guss.) Coincy, J. Bot. (Morot) 12:55. 1898.
Tunica prolifera subsp. *velutina* (Guss.) Briq., Prodr. Fl. Corse 1:570. 1910.
Petrorhagia prolifera subsp. *velutina* (Guss.) O. Bolòs & Vigo, Butl. Inst. Catalana Hist. Nat., 38 Bot. 1:87. 1974. TYPE: SICILY; "Val di Mazzara, e Val di Noro, Madonie" (Fl. NAP?), *vide* Meikle (1977). Original material not seen.
Dianthus ambiguus Nicorra, Prodr. Fl. Messan. 123. 1883., *nom. illeg.*, non Salisb., Prodr. 303. 1796., non Pančić, Fl. Serbiae 178. 1874, nec Pančić, Nova Elem. Fl. Bulg. 185. 1886. TYPE LOCALITY: SICILY. Original material not seen.
Dianthus sartorii Fruehl ex Nyman, Consp. Fl. Eur. 107. 1878. *Dianthus velutinus* var. *sartorii* (Fruehl) F. Williams, J. Bot. 23:347. 1885. Original material not seen.
Dianthus diminutus sensu Desf., Fl. Atlant. 1:345. 1799, non L.
Dianthus prolifer sensu Friedr., Reise. 270. 1838, non L.
Petrorhagia prolifera sensu Shinn., Sida 3:345. 1969, *sensu* Correll & M. Johnston, Contr.

- Texas Res. Found., Bot. Stud. 6:613. 1970, *et sensu pro parte* Kartesz & Kartesz, Syn. Check. Vasc. Flora. 153. 1980, non (L.) P. Ball & Heyw.
Tunica prolifera sensu Munz & Keck, Calif. Fl. 293. 1959, *et sensu* H. St. John, Pac. Trop. Bot. Gard. Mem. 1:160. 1973, non (L.) Scop.

Annual. Stems often simple or sometimes branched near the base, 9.5 – 60(CA)-91(TX) [commonly 25 – 40] cm tall; all internodes glabrous or nearly so (most Oklahoma and Texas collections), or middle internodes densely glandular-tomentose (most California collections). Leaves linear to linear-oblong, 10 – 60 mm long, 1.5(2) mm or less wide, lowermost oblanceolate, often broader (to 5 mm wide), 3-veined, margin scabrous; leaf sheath variable in length, (3)4-6(9) mm long, 2-3 times as long as broad. Inflorescence capitate as in *P. prolifera*, (10) 14 – 20 mm long, 6 – 10(23) mm wide, but with tips of all inflorescence bracts mucronate, reddened when young. Sepals 3-veined, outer surface often scabrous, especially along veins; margin glabrous. Petals clawed, pink or purplish (rarely white); primary veins 3 per petal, "pencilled crimson at base of limb" (Meikle, 1977), central vein may fork in bifid petals and at least 2 minor veins may also be colored, producing 5 – 6 dark veins; apex obcordate or (more commonly) bifid. Anthers blue or pink; pollen 32 μ m (Candau, 1980). Seeds semipyriform, more angled (concave-convex) than above species, surface covered with conical papillae, 1.0 – 1.3(1.4) mm long, 0.7 – 0.8(1.0) mm broad. $2n = 30$ (Böcher et al., 1955; Thomas & Murray, 1983). Figs. 6, 10, and 16.

One of the most obvious morphological characters, stem pubescence, proves problematic in *P. velutina*. The absence of pubescence on many collections from Oklahoma and Texas has led to repeated misidentifications, as mentioned earlier. Maire (1963) considered glabrous-stemmed plants to represent a distinct variety, a concept not recognized by Ball and Heywood (1964). I agree it is best not to add a formal infraspecific name to the glabrous plants since this character does not correlate with differences in seed testa and, as Briquet (1910) observed in Corsica and I observed in Texas, glabrous- and glandular-stemmed plants may grow together.

The consideration of *P. velutina* as a subspecies of *P. prolifera* by Bolòs and Vigo (1974) is based on the treatment of Briquet (1910) and reflects the ideas of Malinvaud (1893), who suggested placing all members of the "*prolifera*" group within a single species, limiting "secondary units" to subspecies and varieties. Acceptance of such a classification would minimize the importance of distinct karyotypic differences between *P. prolifera* and *P. velutina* shown by Böcher et al. (1955) and Thomas and Murray (1983) and

the breeding barriers isolating *P. velutina* from all other taxa in section *Kohlruschia* noted by Thomas and Murray (1981).

Four common names have been used for *P. velutina* in North America, although in each case, the epithet *prolifera* is used in the accompanying scientific name. Howell (1962) used Childing Pink when describing plants from Butte County, California. St. John (1973) cited Tunic Flower in reference to plants in Hawaii, which would be introduced *P. velutina* according to Ball and Heywood (1964). Niehaus (1974) used Proliferous Pink, while Niehaus and Ripper (1976) preferred Wild Carnation as the common name for plants in the Sierra Nevada foothills. The epithet "*velutina*" is an obvious reference to the "dense, glandular-tomentose indumentum" on most middle internodes of the typical *P. velutina* (Ball & Heywood, 1962).

FLORAL BIOLOGY: Thomas and Murray (1981) reported that *P. velutina* is normally autogamous, finding that the timing of anthesis and stigma receptivity coincide and that the average lengths of filaments and styles are very similar. Some cross-pollination may occur if vectors are present since the stigmas do protrude above the corolla.

ECOLOGY AND DISTRIBUTION: *P. velutina* is native to the Mediterranean region, with introduced populations found in Australia, Hawaii, and South Africa (Ball & Heywood, 1964). Two specimens have been seen from Chile (Junge 2636, US: Looser 4349, GH), indicating an introduction to South America. Except for two cultivated records, the North American distribution of *P. velutina* is restricted to northern California (Fig. 17), southeastern Oklahoma, and eastern Texas (Fig. 18.).

Nearly all *P. velutina* collections from Texas and Oklahoma came from roadside localities, with little evidence of invasion of adjacent communities. *P. velutina* is also a roadside plant in northern California, although Frenkel (1970) did not list it as a "high presence species" in his study of roadside vegetation. An inspection of collection labels revealed that *P. velutina* has left the roadside and has invaded at least two of the Woodland-Savanna communities described by Munz and Keck (1949, 1950); the Northern Oak Woodland and the Foothill Woodland as they occur in the North Coast ranges and the Sierra Nevada foothills. The presence of a Mediterranean climate (hot, dry summer; mild rainy winter) in California (Gleason and Cronquist, 1964) may be a positive factor in the expansion of *P. velutina* into oak and oak-pine woodlands, valley meadows, and stream banks. Flowering is noted from early April to early June.

HISTORY OF INTRODUCTION: It is evident from both time and morphological considerations that *P. velutina* has been introduced to North

America at least twice (excluding known cultivations); once in northern California and once in eastern Texas. For this reason, a separate account will be presented for each region.

CALIFORNIA: It appears that *P. velutina* was introduced in northern California in the late 1920's, with six collections noted in a 30 mile \times 20 mile \times 20 mile triangular area, including parts of NE Butte, SW Nevada, and NE Yuba counties between 1927 and 1940 (Fig. 17). None of the collection labels indicated cultivated origin; two were gathered along roadsides, three from streamside areas, while the sixth was found on rocky hillocks west of a town. The literature is of little help on this point. Robbins (1940) listed only one location for *P. velutina* (*T. prolifera*), indirectly citing Yates' collection (Yates 3616 in 1933, UC) in Yuba County. Wolf (1938) summarized the situation when he wrote "we have recently found it in California [Wolf 8632 in 1937] where it apparently has been established for many years, but has been overlooked by collectors."

TEXAS: Most evidence points to a 1967–1968 introduction of *P. velutina* to eastern Texas. The only contradictory report is the listing of *Dianthus prolifer* for region 2, the Coastal Prairies, by Cory and Parks (1937). I have seen no specimen to document this statement, no recent collections of *P. velutina* from this area, and furthermore, Gould (1962) did not list the species as present in Texas.

Shinners (1969) noted the "sudden appearance" of *P. velutina* (his *P. prolifera*) in May, 1968 along highways in east Texas which "I have traveled almost yearly for two decades without finding it." He postulated it could have been introduced as a result of state highway department planting of rye grass, *Lolium perenne* L. var. *italicum* (A. Braun) Parnell. Correll and Johnston (1970) concurred, noting "its very recent introduction into Texas, probably in contaminated rye grass seed."

On the labels of the earliest Texas collection seen (*D. S. and H. B. Correll* 35641; CM, LL), the Corrells suggested another vector when they wrote: "probably introduced with Italian clover seed by Texas Highway Dept." Italian clover, *Trifolium incarnatum* L. (per Bailey et al., 1976), is listed by Turner (1959) as being "cultivated in the eastern part of the state, but occasionally escaping", his map showing its presence in eight counties. The Corrells' suggestion may be the "correct" source for several reasons. The Texas State Department of Highways and Public Transportation did spread *T. incarnatum* seed in the 1960's, the species "generally seeded throughout the eastern one-third of Texas, from Dallas eastward", although the seeding plans have been revised "to the extent that *Trifolium incarnatum* is no longer specified for our current seeding practices." (B. C. Blaschke, pers. comm.).

Trifolium fragments were present at the base of plants in four collections seen spanning four neighboring counties and three growing seasons. Finally, personal observations suggest *T. incarnatum* as the vector, the species being a dominant associate at each collection site, while *Lolium perenne* was absent from four of the sites visited (Rabaler 351, 352, 353, and 356).

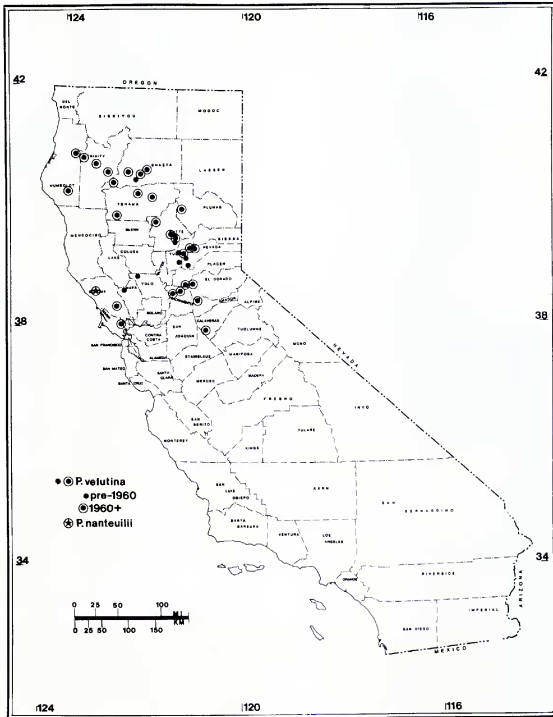


FIG. 17. Distribution of *Petrorhagia nanteuillii* and *Petrorhagia velutina* in California.

CURRENT STATUS: Since the California and Texas-Oklahoma populations still appear as distinct entities with no range overlap yet documented, the status of *P. velutina* in these areas will be treated separately.

CALIFORNIA: The list of specimens cited below includes the earliest and most recent collections seen from a given county. Once again, the floristic manuals present a vastly different picture from that of the specimens examined (also see Fig. 17). As noted previously, Robbins (1940) listed *P. velutina* for Yuba County. Munz and Keck (1959) described *Tunica prolifera* as "occasional as a weed reported from Butte, Nevada, Yuba cos." Raven (1965) cited the same distribution in a note giving the correct name as *P. velutina* based on Ball and Heywood (1964) and a confirming identification of the California material by Heywood. Munz (1968) added Sacramento and Shasta Counties and changed the name to *Kohlruschia velutina* [Howell (1972) adopted *Petrorhagia velutina* in his commentary on Munz (1968)].

Nichaus (1974) stated that *T. prolifera* (*P. velutina*) was "common as a pink mass under foothill oaks, Nevada Co. and north below 3000 ft."; a very accurate generalized description of the current status of *P. velutina* in California. He went on to note that this species is "rapidly spreading throughout the foothills", a statement that is easily verified by arranging the specimens examined in chronological order by date of collection. The following pattern appears: pre-1939, 3 counties; 1940-1949, 1 added; 1950-59, 2 added; 1960-69, 6 added; 1970-on, 5 more counties added. This totals 17 counties, 15 of which are represented by collections dating from after 1960, 10 from 1970 or later. It is evident that this species is fully naturalized and probably still expanding into other areas of northern California.

TEXAS: The earliest collection seen from a given county is included in the list of specimens cited below. Most specimens of *P. velutina* examined were collected between 1968 and 1971. During those years, it apparently spread rapidly, with eight additional counties added to the four counties represented by the 1968 collections (Fig. 18). Correll and Johnston (1970) described it as "an extremely aggressive plant," noting that it has spread to much of east Texas. My observations in 1980 confirmed that statement, with a large number of plants seen along the roadsides in eight counties during my brief visit. The stature and density of *P. velutina* at some sites clearly suggested a naturalized species. Collections made in three counties (Cherokee, Henderson, and Rains) represented new records, indicating that *P. velutina* was still invading additional sites. Two 1983 collections from southeastern Texas roadsides (Colorado and San Jacinto counties) and a

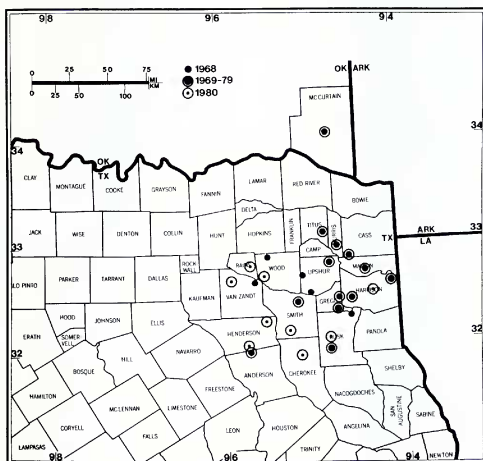


FIG. 18. Distribution of *Petrorhagia velutina* in Oklahoma and Texas, 1968-1980. 1983 collections from Colorado and San Jacinto counties, Texas excluded.

1978 collection from a roadside in southeastern Oklahoma suggest that this species may be more widely distributed than either literature or collections currently indicate.

Representative specimens: UNITED STATES. CALIFORNIA. AMADOR CO.: Bank of Consummes River, S of Larrobe, 5.6 mi N of Ca 16 jct., 2 May 1974, *McNeal* 1456 (NY). BUTTE CO.: Bidwell Bar bridge, 10 mi E of Oroville, 10 May 1940, *Cantelow* 3078 (RSA); sandy grassland along CA 99, 11 mi N of Chico, 18 Apr 1978, *Joslin* 11 (CM); Bidwell Bar, 21 Apr 1929, *Wilkins* s.n. (UC). CALAVERAS CO.: Wooded slope, 4 mi SE of Milton, 3 May 1963, *Breedlove* 4768 (SMU). EL DORADO CO.: Open grassland, Folsom Lake State Park, 18 Apr 1964, *Huether* 34 (DAV); E shore of Folsom Lake, 5 mi NE of Folsom, 1 May 1960, *Simonds* s.n. (CDA). HUMBOLDT CO.: Gravel bank along Eel River floodplain, 20 Apr 1973, *Anderson* s.n. (HSC). MARIN CO.: Along road to Black Point, 1.5 mi NE of Ignacio, 20 Apr 1971, *True* 6477 (CAS, JEPS, NY). NAPA CO.: Valley clay, 6 mi N of Aetna Springs, Pope

Valley, 8 May 1948, *Smith s.n.* (DAV). NEVADA CO.: Roadside bank, Hwy 20, 7 May 1938, *Heller 15077* (ILL, MO, NY, POM, UC); rocky roadside bank along CA 49, 2 mi N of North San Juan, 4 May 1963, *Rice 176* (NCU). PLACER CO.: Edge of beach, Folsom Reservoir, 2 mi N of Folsom, 4 May 1964, *Clegg 27* (DAV); near old homestead, Orangevale, 26 Apr 1976, *Van Ess 3485* (SACT). PLUMAS CO.: Rocky slope near Murphy Creek along CA 70, 2.2 mi W of Belden, T25N, R6E, S26, SW1/4, 9 Aug 1980, *Rabaler 514* (CHSC, GH, HHH, MSC, ROPA, UC). SACRAMENTO CO.: 0.25 mi S of fish hatchery, American River, 20 Apr 1963, *Gustafson s.n.* (SACT). SHASTA CO.: Dry grassland, 1.5 mi N of Anderson, 12 Apr 1952, *Cutright 32* (JEPS); oak-pine woodland, Co. Rd. A16, 9.7 mi NE of CA 36, T30N, R8W, S33, 9 Apr 1978, *Smith, Sawyer, and Nelson 9719* (HSC). SONOMA CO.: Grassy area, W slope of Sonoma Mtn, Osborn Nature Conservancy Preserve, E of Rohmert Park, May 1979, *Serpa s.n.* (MSC, OSH, ROPA). TEHAMA CO.: Along creek bank at rest area, 1-5, 9 mi S of Shasta Co. line, T28N, R4W, S25, 26 May 1977, *Halse 1585* (WTU); bank of Reeds Creek at Paskenta Road, 30 Apr 1967, *Wheeler 20* (CHSC). TRINITY CO.: Along CA 299 at Hayden Flat Campground, T5N, R7E, S24, 17 May 1975, *Smith 8118* (HSC); grassy canyon slope, 3 mi SW of Douglas City, 22 Apr 1965, *Weber 12284* (DAO, ILL). YOLO CO.: Cache Creek cañon, along CA 16, 2.5 mi NW of Rumsey, 22 Apr 1958, *Bacigalupi, Mason, and Mason 6277* (JEPS). YUBA CO.: Oak woodland, Foothill Range Exper. Station, 19 Apr 1966, *Carr 160* (MIN); flat W of North San Juan, 11 May 1927, *Mason 3735* (JEPS, UC); edge of creek bed, 2 mi N of Brown's Valley, 13 May 1937, *Wolf 8632* ([CAS], [DS], GH, [LA], NY, POM, RSA, UC, US); Spencerville Rd. at Indian Springs, T15N, R7E, S19, 23 May 1933, *Yates 3616* (UC). OKLAHOMA. McCURTAIN CO.: Along roadside near Yanubbee Creek, US 259, 2.5 mi N of Broken Bow, 30 Apr 1978, *Taylor 25906* (DUR, LSU, MO). TEXAS. ANDERSON CO.: Roadside, TX 19, 12 mi S of Athens, 22 May 1969, *Barclay 3054* (NA). CASS CO.: Roadside, 3.2 mi SW of Avinger, 28 Apr 1970, *Shinners 33022* {*Southern Appalachian Botanical Club 2618*} (FLAS, KNK, MASS, MICH, MSC, NLU, SMU, WVA). CHEROKEE CO.: Red sandy clay along US 79, 3.2 mi W of New Summerfield, 2 May 1980, *Rabaler 346* (MIN, MSC, NY, SMU). COLORADO CO.: Along I-10, 1 mi W of FM 949, 15 May 1983, *Brown 6033* (SMU). GREGG CO.: Roadside, US 259, Kilgore, 12 May 1969, *Shinners 32631* (SMU). HARRISON CO.: Roadside, W side of Hallsville, 13 May 1969, *Shinners 32635* (MSC, SMU). HENDERSON CO.: In red sandy clay along E side of TX 19, 10 mi S of Athens, 1 May 1980, *Rabaler 330* (GH, MSC, SMU, UC). MARION CO.: Sandy clay road shoulder, TX 49, 2.2 mi W of Jefferson, 13 May 1969, *Shinners 32643* (MSC, SMU). MORRIS CO.: Re-graded road cut, TX 11, Daingerfield, 21 Apr 1969, *Shinners 32597* (SMU, TENN). RAINS CO.: Roadside, E side of US 69; 6.4 mi NW of Alba, 3 May 1980, *Rabaler 353* (MSC, SMU). RUSK CO.: Roadside, 4.2 mi NW of Tatum, 5 May 1968, *Shinners 32222* (FLAS, MASS, MSC, SMU, TENN, VDB). SAN JACINTO CO.: along TX 2025, 2 mi S of TX 150, 27 May 1983, *Brown 6136* (SMU). SMITH CO.: Harris Creek Cemetery, W of Winona, 22 May 1971, *Thomas 23207* (AUA, DUL, ILL, NLU, TENN). TITUS CO.: Roadside, TX 49, 7 mi E of Mt. Pleasant, 28 Apr 1971, *Amerson 389* (SMU). UPSHUR CO.: Road shoulder, 5.8 mi ESE of Big Sandy, 7 May 1968, *Shinners 32233* (MASS, SMU); grassy roadside, TX 155, 5 mi W of Ore City, 1 May 1969, *Correll 37154* (FSU, GH, LL, MICH, NA, NCU, NY, OKLA, TEX). VAN ZANDT CO.: Roadside, 2.8 mi E of Grand Saline, 7 May 1968, *Shinners 32238* (MASS, SMU). WOOD CO.: Near pond along Farm Rte 514, 4 mi E of Yantis, 25 Apr 1968, *D. S. and H. B. Correll 35641* (CM, LL).

Cultivations: MARYLAND. PRINCE GEORGES CO.: In Glenn Dale Introduction Garden (seed from Turkey), 23 June 1938, *Cowgill 808* (BH, GH, MICH, NA). PENNSYLVANIA. PHILADELPHIA CO.: cultivated, Mehans Garden, without date, *Burk s.n.* (PENN).

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